New fossil material with a redescription of the extinct Condor *Gymnogyps varonai* (Arredondo, 1971) from the Quaternary of Cuba (Aves: Vulturidae)

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Abstract.—New material of the Cuban Condor, originally described at *Antillovultur varonai* (Arredondo, 1971), indicates that it is definitely referable to the genus *Gymnogyps,* but possesses other unique features that support its status as an extinct endemic species. It is characterized by distinct cranial and premaxillary features that are associated with more powerful musculature for feeding. These features include dorso-ventral deepening of the skull, long and massive occipital processes, a large occipital condyle, and a more vaulted and broad rostrum compared with the living species *G. californianus.* Postcranial bones differ little from the living California Condor except in being larger and more robust. The Cuban Condor may have evolved relatively rapidly after a mainland population of *G. kofordi* or *G. californianus* reached the island and became specialized on the limited large prey available there during the Pleistocene.

Resumen.—Nuevo material del Cóndor Cubano, originalmente descrito como *Antillovultur varonai* (Arredondo, 1971), indica que éste es definitivamente referible al género *Gymnogyps,* pero posee caracteres únicos que sustentan su estado como especie endémica extinta. Se caracteriza por rasgos craneales y premaxilares distintivos, asociados a una musculatura potente, dado su modo de alimentación. El cráneo presenta una mayor profundidad dorso-ventral, procesos occipitales largos y masivos, cóndilo occipital grande, y rostro más ancho y arqueado, en comparación con la especie viviente *G. californianus.* Los huesos postcraneales difieren poco del Cóndor de California, excepto por ser mayores y más robustos. El Cóndor Cubano pudo haber evolucionado relativamente rápido a partir de la colonización de la isla por una población continental de *G. kofordi* o *G. Californianus,* que se especializó en el consumo de las limitadas carroñas derivadas de la megafauna disponible en Cuba durante el Pleistoceno.

Condors are large members of the family Vulturidae (=Cathartidae auct.) that appear to have originated in North America and later colonized South America (Emslie 1988). The only condor known outside the continental mainland of the Americas is the Cuban Condor *Gymnogyps* ("*Antillovultur*") *varonai* (Arredondo 1971, 1976; Suárez 2000), providing evidence for the ca-pability of these scavengers to cross large bodies of water (see Tambussi & Noriega 1999). The genus *Gymnogyps* Lesson was most diverse in the Pleistocene and only the California Condor (*G. californianus*) survives today (Emslie 1988). The earliest record of the genus is from late Pliocene (Blancan) deposits of Florida (Emslie 1988, 1998). In addition, the fossil species *Gym-*

nogyps kofordi is known from the early Pleistocene (middle Irvingtonian) of Florida (Emslie 1988). The only other fossil species in this genus are *G. howardae* from the late Pleistocene asphalt deposits of Talara Tar Seeps, Peru (Campbell 1979) and *G. varonai,* originally described as *Antillovultur varonai* (Arredondo, 1971) from Quaternary cave deposits of Cuba. The supposed species, *G. amplus,* from late Pleistocene asphalt deposits of Rancho La Brea (Rancholabrean) described by Miller (1911), is now considered to be a junior synonym of *G. californianus* and was a large, Pleistocene temporal subspecies (Emslie 1988).

Recently, Suárez (2000) reviewed newly recovered fossil material and the generic status of the Cuban Condor as well as its paleodistribution and possible origin. As a result of this review, the monotypic and endemic genus "*Antillovultur*", in which the species *varonai* was originally described, was considered congeneric with *Gymnogyps,* an assumption that had been made by other authors (Olson 1978, Emslie 1988).

Certain cranial and postcranial characters of *Gymnogyps varonai* were described by Suárez (2000), but were limited to only the generic, rather than the specific, position of the Cuban bird. Although some cranial features agreed with those described for fossil specimens of *G. californianus amplus* and *G. kofordi,* no direct comparisons were made with these taxa and the specific status of the Cuban bird has remained unclear since that time. Here we provide more detailed comparisons of the Cuban Condor with other fossil and living species.

Materials and Methods

Material examined.—The same specimens of the Cuban Condor, *Gymnogyps varonai,* listed with localities and depositories by Suárez (2000). Proximal end of a right radius, Instituto de Ecología y Sistemática, La Habana, Cuba (IZACC 400–813). Fossils from the paleontological collection of the Museo Nacional de Historia Natural, La Habana, Cuba (MNHNCu), recovered in asphalt deposits Las Breas de San Felipe (San Felipe II), 5.5 km west of Martí, Municipality of Martí, Matanzas Province, Cuba (for description and discussion of the chronology of this deposit see Iturralde-Vinent et al. 2000): fragmentary premaxillae (MNHNCu P4594, MNHNCu P4595), right coracoid (MNHNCu P4596), proximal right carpometacarpus (MNHNCu P4597) and distal left tarsometatarsus (MNHNCu P4598). Other fossil material examined is housed at: Museo Polivalente de Sagua la Grande, Villa Clara (MPSG), Collection of Oscar Arredondo, La Habana (OA), and Collection of William Suárez, La Habana (WS).

Comparative material of the living, post-Pleistocene subspecies of the California Condor, *Gymnogyps c. californianus* examined at the National Museum of Natural History, Smithsonian Institution (USNM), include the following skeletons: 13823, 17033, 17946–50, 345225, 346582, 489359, 489406, 489755, 492447. Comparisons with specimens of the fossil California Condor, *G. c. amplus* from Rancho la Brea, were made with the extensive collections of the George C. Page Museum, Los Angeles, California. Specimens of *G. kofordi* from Florida Museum of Natural History, Gainesville (UF) include the following paratypes: distal right ulna UF 63516; left femur UF 63513; distal left tarsometatarsus UF 31904. Casts of the holotypical right tarsometatarsus UF 63512, and paratypical fragmentary cranium UF 63517, also were used for comparison with this species. Osteological terminology herein follows that of Howard (1929), Fisher (1944), and Jollie (1976–1977). Measurements were taken with a vernier caliper to the nearest 0.1 mm, following the methods of Fisher (1944) and Emslie (1988) for the cranium. Measurements designated with a plus sign (+) are from specimens with wear and abrasion, and are approximate.

Systematic Paleontology

Class Aves
Order Ciconiiformes
Family Vulturidae (Illiger, 1811)
Genus *Gymnogyps* Lesson, 1842

Generic characters of *Gymnogyps* (Emslie 1988) found in the Cuban specimens (Suárez 2000) are: cranium in dorsal view with constriction at postorbital, supraorbital edge convex, postorbital pit deep, upper mandible short and robust with nasal bar near the horizontal position in lateral view, bony circle formed by medial septum. Carpometacarpus with large proximal symphysis (see Howard 1974); tarsometatarsus with concave surface of posterior shaft and with well-developed posterior protrusion on external cotyla.

Gymnogyps varonai (Arredondo, 1971)

Amended diagnosis.—*Gymnogyps varonai* differs from *G. californianus* Say, *G. kofordi* Emslie, and *G. howardae* Campbell (cranial material unknown in this species), in having: premaxillary short, broad and deeply vaulted, positioned near the level of the external nares (premaxillary larger and less vaulted in *G. californianus*; shorter, but less vaulted in *G. kofordi*), nasal bar very short, broad and flat (nasal bar relatively more slender, less broad and more rounded dorsally, not as flat in *G. californianus*; more slender, less broad, and constricted at the midpoint in *G. kofordi*), alinasal large, wide and flat, occupying more space in a shorter narial opening (alinasal small and less wide and flat, with narial opening larger in *G. californianus*; narial opening very large in *G. kofordi*); interpalatal space thin, maxilla wide, and maxillopalatines with a thin space between them so that they nearly touch at the mid line (interpalatal space wide in both *G. californianus* and *G. kofordi*); cranium high, with strong protrusion of the supraoccipital, large and massive occipital processes with lateral areas beside supraoccipital protrusion thin and high (su-

praoccipital less protruding, with lateral areas wide and not as high in *G. c. californianus*; supraoccipital protrusion similar in *G. c. amplus* and *G. kofordi,* but with lateral areas wide and not as high), space between both temporal fossae small and flat (space between both temporal fossae wide and less flattened in *G. c. californianus* and *G. kofordi*), nuchal crest rostrally placed causing the area between this crest and the postorbital process to be very short (larger in specimens of *G. c. amplus* and *G. kofordi*), interorbital space wide and flat (narrower and more rounded in *G. californianus* and *G. kofordi*), postorbital processes short with caudal orientation (postorbital processes larger with rostral orientation in *G. californianus*; larger with slightly more rostral position in *G. kofordi*); temporal fossa short antero-posteriorly, but deep and in general high and wide. Distal end of ulna flat in external-distal surface, external condyle short and wide, distal radial depression large and pneumatic, carpal tuberosity large (rounded external-distal surface, external condyle large with distal radial depression small, less pneumatic in *G. californianus*; large and pneumatic distal radial depression in *G. kofordi*). Tibiotarsus with internal and external cnemial crests weakly developed and projected with reduction of muscular insertions, anterior and posterior intercondylar sulcus very thin causing the external condyle in distal view to be shorter and more voluminous. Tasometatarsus relatively short and robust, distal foramen placed low on shaft though this feature is variable.

Comparative Description

The Cuban Condor is particularly distinct from from *G. californianus* and *G. kofordi* in having a deeper, more laterally-compressed cranium with exaggerated occipital and opisthotic processes, and the more rostal placement of the nuchal crest (Fig. 1). The rostrum (Fig. 2) also is more robust and deeply vaulted, with the dorsal surface bulging slightly above the level of the nasal

Fig. 1. Partial skull (MPSG 21) of *Gymnogyps varonai* (middle) in comparison with the equivalent element in fossil (right) and living (left, USNM 492447) *G. californianus,* in dorsal (A) and lateral (B) views. Scale bar = 1 cm.

bar, more so than in *G. californianus* and *G. kofordi.* The mandible is similar to *Gymnogyps californianus* except in being generally more robust, with larger and blunter articular processes. This element is not known in *G. kofordi.*

Postcranial characters of the Cuban Condor that differ from *G. californianus* include coracoid with higher and more massive furcular facet and coraco-humeral surface, attachment for anterior articular ligament in distal humerus extends farther distal-externally on shaft, presence of small pneumatic foramen on proximal shaft of radius below capital tuberosity (similar to *G. kofordi*), distal ulna with prominent shelf on the carpal tuberosity with a large foramen located distal to the shelf (similar to *G. kofordi*) and external condyle that tapers and extends less proximally, tibiotarsus (Fig. 3) with relatively long fibular crest and distal end with narrow intercondylar fossa when viewed distally, and tarsometatarsus (Fig. 4) with long and narrow middle trochlea (similar to *G. kofordi*).
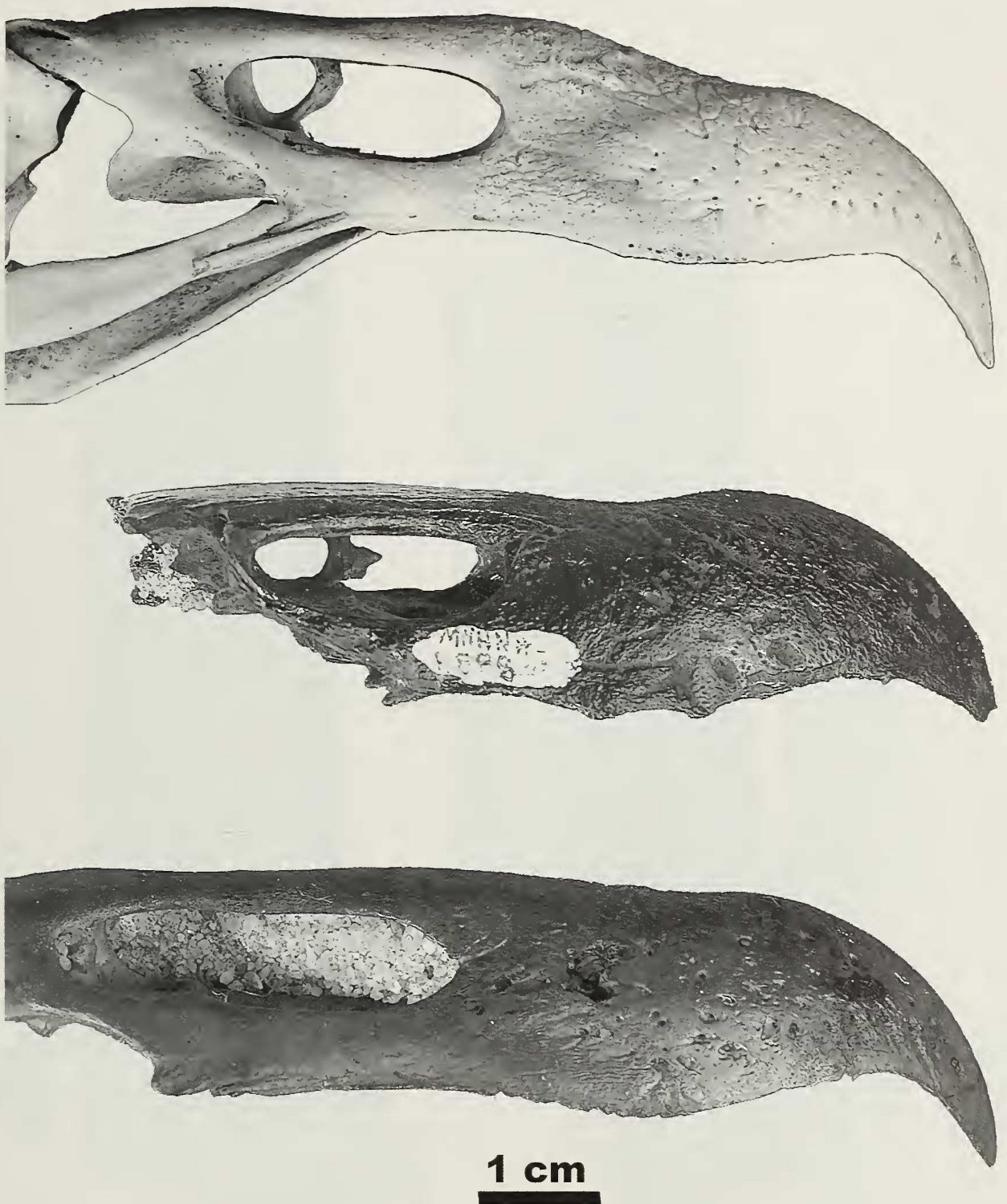
Measurements (mm).—Cranium (MPSG

Fig. 2. Lateral view of the rostrum (upper mandible; MNHNCu P4613) of *Gymnogyps varonai* (middle) in comparison with the equivalent element in living (top, USNM 492447) and fossil (bottom) *G. californianus.* Scale bar = 1 cm.

21): temporal breadth, 43.2; cranial height, 38.8; postorbital position 51.9; postorbital breadth, 43.0; occipital breadth, 33.7. Premaxilla (MNHNCu P4613, formerly P588): breadth, 26.5; narial length, 21.9; narial breadth, 8.1; least breadth of nasal bar, 10.4; breadth of interpalatal space, 8.7;

MNHNCu P4594: least breadth of nasal bar, 11.1.

Coracoid (MNHNCu P4596): total length, 98.9; least breadth at midpoint, 17.0; depth at level of midpoint of glenoid facet, 21.8. Humerus (MPSG 30 and 31): proximal breadth, 53.0 and 52.6, respec-
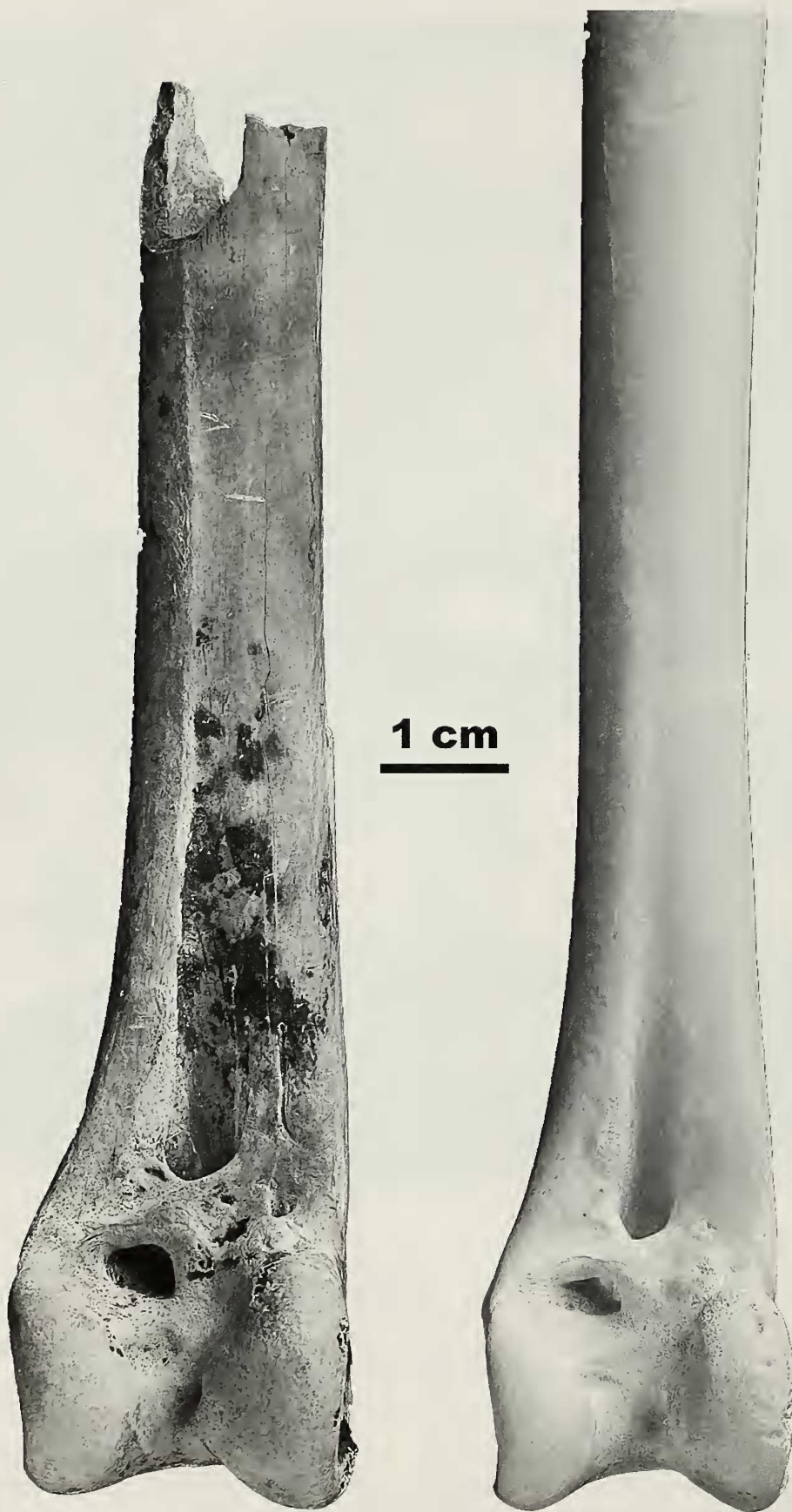
Fig. 3.   Distal left tibiotarsus (MPSG 43) of *Gymnogyps varonai* (left) in comparison with the equivalent element in the living *G. californianus* (right, USNM 492447). Scale bar = 1 cm.

Fig. 4.   Left (middle, WS 125) and right (right, WS 978) tarsometartarsi of *Gymnogyps varonai* in comparison with fossil *G. californianus* from Rancho la Brea (left). Scale bar = 1 cm.

tively; depth of head, 18.0 and 18.2; IZ-ACC P80: least breadth and depth of shaft, 20.0 and 16.0; distal breadth and depth, 47.4 and 26.4; MPSG 32 and 33: distal breadth, 49.0 and 48.7, respectively; MPSG 33: distal depth, 25.1. Ulna (MPSG 34): distal breadth and depth, 22.9 and 23.3. Radius (MPSG 36 and 37, IZACC 400–813): greatest diameter at proximal end, 16.9, 15.7, and 15.8, respectively; MPSG 35: distal breadth, 23.6. Femur (OA 3202): total length, 141.0; proximal breadth, 37.3; depth of head, 17.0; least breadth shaft, 17.4; distal breadth, 35.6; MPSG 38: proximal breadth, 35.7; depth of head, 17.8. Tibiotarsus (MPSG 42): breadth of proximal

end through articular surface, 28.3; MPSG 43: least breadth and depth of shaft, 14.2 and 11.6; depth of external condyle, 23.5; distal breadth, 26.2; MPSG 41: length of fibular crest, 53.2. Tarsometatarsus (WS 125): proximal breadth, 25.7+; least breadth and depth of shaft, 15.0 and 8.8; MPSG 45e: proximal depth, 22.4; least depth shaft, 7.1+; breadth and depth of trochlea for digit 4, 8.2 and 16.3+; WS 978: least breadth and depth of shaft, 14.7 and 8.8; distal breadth, 32.2+; breadth and depth of trochlea for digit 2, 9.6+ and 13.1+; breadth and depth of trochlea for digit 3, 11.4+ and 16.5; breadth and depth of trochlea for digit 4, 7.6 and 14.9+; MNHNCu P4598: distal breadth, 33.0; breadth and depth of trochlea for digit 2, 10.0 and 13.4; breadth and depth of trochlea for digit 3 depth, 11.7 and 16.6; breadth and depth of trochlea for digit 4, 8.3 and 13.4; OA 847: breadth and depth of trochlea for digit 4, 8.0 and 15.9.

Discussion

The Cuban Condor differs from other fossil and living *Gymnogyps* mainly in features of the skull. The long and massive occipital processes, the shape of the braincase, and the relatively large occipital condyle indicate that this species had large neck vertebrae and greater musculature in the head and neck associated with feeding. In addition, the relatively robust bill indicates that the Cuban Condor was more powerful and presumably could tear thick skin and sinew more easily than other condors of this genus. The more rostral placement of the nuchal crest in the Cuban Condor compared to other fossil and living *Gymnogyps* also is probably related to this more powerful feeding ability (see also Hertel 1995 for a description of cranial features related to scavenging). Postcranially, the Cuban species shows few differences in characters with other condors except for being relatively larger and more robust than *G. californianus californianus* or *G. kofor-*

di, and more similar to *G. c. amplus* (Suárez 2000).

The Cuban Condor may have descended from *Gymnogyps kofordi* or *G. californianus,* both of which occurred in Florida (Emslie 1998, Suárez 2000). We hypothesize that a population of one of these species reached Cuba in the early to late Pleistocene and quickly diverged into the endemic form. Although fossil evidence is lacking for the presence of condors in Cuba prior to the late Pleistocene, *G. varonai* shares more cranial and some postcranial similarities with *G. kofordi* than with *G. californianus,* although the rostrum is most similar to that of *G. californianus,* especially in the configuration of the nasal bar.

Once established in Cuba, rapid divergence from its Florida counterpart would be facilitated by its insular isolation. In addition, we speculate that limited large prey available at that time also might facilitate rapid morphological change in the cranial and bill regions. Large vertebrates known from the late Pleistocene of Cuba such as sloths [*Megalocnus, Parocnus* (=*Mesocnus*), *Acratocnus* (=*Miocnus*)], large rodents, and tortoises (*Geochelone*) were the main food sources for *Gymnogyps* (Suárez 2000). It is likely that the condors began to specialize on carcasses of these species and the thick hides of the sloths, and the hard carapaces of the turtles, selected for a more powerful feeding apparatus in Cuban Condors than in mainland species with more varied food sources.

Strong competitive interactions at carcasses with other scavenging birds identified in the fossil record of Cuba (Suárez 2001), including many raptorial species that were quite diverse in the Quaternary here, also may have increased the selective pressure for the robust cranial characters of *Gymnogyps varonai.* A more powerful bill for holding onto prey remains during interactions at a carcass may have made the Cuban Condor more competitive if food was limiting. Additional research on the functional morphology of the unique cranial

characteristics of *G. varonai* with further studies of the extensive undescribed material of raptors from the Quaternary of Cuba are needed to further address this issue.

Acknowledgements

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